Pleioptygmatidae, a New Family of Mitriform Gastropods (Prosobranchia: Neogastropoda)

James F. Quinn, Jr.
Florida Marine Research Institute
Department of Natural Resources
100 Eighth Avenue S.E.
St. Petersburg, FL 33701, USA

ABSTRACT

A new family of mitriform gastropods is proposed, comprising only the genus *Pleioptygma* Conrad, 1863, based on examination of the foregut of *P. helenae* (Radwin & Bibbey, 1972). *Pleioptygma helenae* is the only known Recent species of this genus, known otherwise only from species from the Neogene of the southeastern United States. The unique configuration of the foregut separates this group from the Mitridae, Costellariidae, Volutidae, and Turridae. Features characterizing Pleioptygmatidae include a proboscis introvert not connected to the head, presence of a proboscis bulb, buccal mass divorced from the proboscis, and hypertrophied rhachidian tooth.

Key words: Pleioptygmatidae; systematics; *Pleioptygma helenae*; anatomy.

INTRODUCTION

The genus *Pleioptygma* Conrad, 1863 (type species *Voluta carolinensis* Conrad, 1840), comprises a small group of species with medium to large (attaining 150 mm in length) mitriform shells bearing conspicuous spiral cords, columellar plicae, and siphonal notch. Three nominal species and one subspecies [*P. carolinense*, *P. lineolatum lineolatum* (Heilprin, 1887), *P. lineolatum saginatum* (Tucker & Wilson, 1933), and *P. prodroma* (Gardner, 1937)] and possibly two additional unnamed species are represented in the Tertiary formations of the southeastern United States (W. G. Lyons, personal communication). Only one Recent species, *P. helenae* (Radwin & Bibbey, 1972), is known. Numerous specimens of *P. helenae* have been collected from the continental shelf off northern Honduras (Caribbean), an area in which several endemic, relict genera have been found (Petuch, 1981, 1982a,b; Houbrick, 1986).

MATERIALS AND METHODS

Prior to the summer of 1983, all known specimens of *P. helenae* were shells that had been carried into lobster pots by hermit crabs. However, through the efforts of Mr. Louis Kotora, a St. Petersburg shell dealer, a live-collected specimen of *P. helenae* (male, shell length 69 mm; figure 1) was obtained from lobster fishermen in July–August, 1983. The specimen, collected near Honduras, was preserved in commercial rubbing alcohol (isopropanol) and brought to W. G. Lyons at the Florida Marine Research Institute, Department of Natural Resources, for examination. The animal was extracted from the shell and given to me by Lyons for dissection. A preliminary report on that specimen was presented at the 1984 American Malacological Union Meeting (Quinn & Lyons, 1984). Subsequently, Mr. Kotora provided another live-collected specimen (female, shell length 107 mm) preserved in rum and collected from the same area as the first specimen. Because the shells were to be maintained intact, the animals were extracted by hooking them with a dental probe and pulling with a twisting motion, with consequent loss of most of the posterior portions of the two animals. This report describes the anatomy of the anterior portions, especially the foregut morphology, and proposes the new family Pleioptygmatidae, based on differences from the foregut morphologies of the Mitridae, Costellariidae, Volutidae, and Turridae.

SYSTEMATICS

Superfamily **Muricoidea** Rafinesque, 1815
(*sensu* Ponder & Warén, 1988)

Family **Pleioptygmatidae** Quinn new family
(type genus *Pleioptygma* Conrad, 1863, Miocene–Recent)

Genus *Pleioptygma* Conrad, 1863
(type species *Voluta carolinensis* Conrad, 1840, Pliocene)

Superfamilial placement follows Ponder and Warén (1988). Foregut anatomy of *Pleioptygma helenae* (Radwin & Bibbey, 1972) (discussed below) suggests a taxonomic ranking equal to that of the Mitridae and Cos-

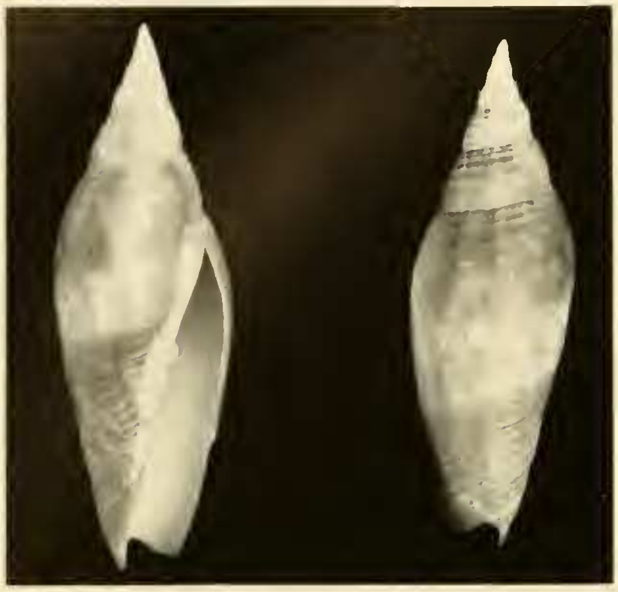


Figure 1. *Pleioptygma helenae* (Radwin & Bibbey, 1972). Ventral and dorsal views of shell of 69 mm male specimen.

tellariidae. *Pleioptygma* is derived from the Greek *pleios*, full, and *ptygma*, a fold. Contrary to common usage, the genus name is neuter, not feminine. Species names in this account are emended accordingly.

Pleioptygma helenae (Radwin and Bibbey, 1972)

Type locality: Gorda Bank, Honduras (here emended).

The type material of *P. helenae* was reported to be from Cay Sal Bank, Bahamas (Radwin & Bibbey, 1972), obtained from lobster pots by a commercial lobster fisherman. Subsequent attempts to collect this species from Cay Sal have failed. Instead, numerous specimens have been collected from the banks off Honduras. I believe the original types were mislocalized and here propose that the type locality be emended to the Gorda Bank, Honduras.

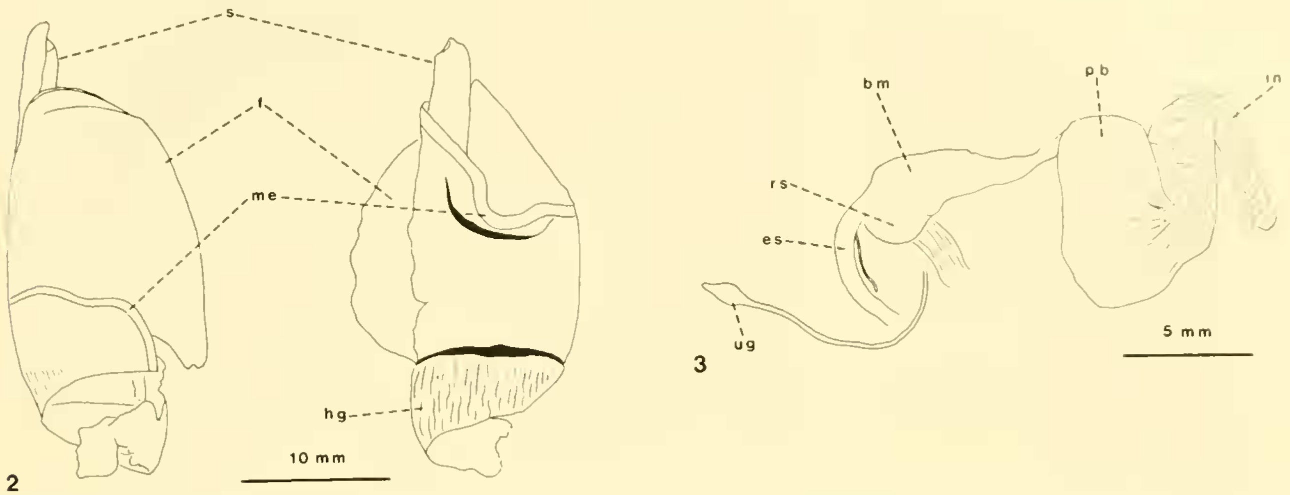
ANATOMY

External features: The remains of the animals after extraction comprise about one whorl each (figure 2); the posterior portion of the mantle cavity and all organs posterior to that were lost. The foot is large, very muscular, uniformly tan to cream in the larger specimen; the smaller is dark chocolate-brown on the sole, fading to grayish buff above. The head is small relative to the foot, with conical snout; the tentacles are short, tapering to rather blunt tips, with conspicuous black eyes located at about midlength. The penis is broad, dorsoventrally flattened, folded to right, and located to the right of the head. The mantle is very thin except for a narrow (1–2 mm wide), muscular band along the edge; the posterior portion and right side are badly torn in both specimens. The siphon is large, thick-walled, muscular, and lacks siphonal appendages. The remains of the ctenidium and osphradium are broad but otherwise unremarkable. The remains of the hypobranchial gland indicate that it is large and rather thick. The columellar muscle is broad and thick.

Proboscis complex: Situated anteriorly is a large, broad introvert (figures 3, 4, 7). The base of the introvert attaches to the right anterior face of the proboscis bulb. The walls of the introvert are thick near the base but rapidly become thin; they are composed principally of circular muscle forming an outer tube or "sheath" and measuring 11–13 mm long when contracted. Distally, the introvert invaginates, runs back through the outer tube/sheath, and enters the proboscis bulb (figure 3). In the larger specimen (figures 4, 7), the introvert turns sharply, runs to the left side of the bulb lumen, then continues diagonally to the right posterior and attaches to a muscular mound on the floor of the bulb. The total length of the contracted introvert is approximately 45 mm. In the smaller specimen, the inner tube of the introvert enters the proboscis bulb, where it is packed in a convoluted mass, exits through the right posteroventral wall of the proboscis bulb, and finally joins the buccal mass. The total length of the introvert is approximately 65 mm.

The proboscis bulb is a large, conspicuous, roughly rectangular structure attached to the floor of the cephalic cavity close to the anterior body wall (figures 3, 4, 7). The bulb of the larger specimen measures 17.0 × 18.5 mm, and that of the smaller 3.5 × 7.5 mm; the greater length of both is perpendicular to the longitudinal axis of the head-foot. The bulb is attached to the cephalic cavity floor by a broad, rather thick band of muscle originating in the foot and inserting along the anterodorsal edge of the bulb. The bulb walls are very thick and are composed of several layers of muscle oriented at right angles to each other. In the smaller specimen, there are four distinct layers oriented transversely-longitudinally-transversely-longitudinally (outer to inner layers, respectively, direction relative to axis of head-foot). The muscle layers of the bulb in the larger specimen are less distinctly demarcated, especially the middle two, because of the addition of much oblique muscle.

Buccal mass: The buccal mass is a muscular, pear-shaped organ lying, *in situ*, on its left side just to the right of the proboscis bulb, its longitudinal axis parallel to the head-foot longitudinal axis and its morphological anterior end topologically posterior (figures 5, 6). The morphological anterior end is separated from the proboscis bulb by a 1.5–2.0 mm length of introvert in the smaller specimen. However, in the larger specimen, the anterior part of the buccal mass extends through the wall of the proboscis bulb and protrudes into the bulb lumen as a prominent mound to which the introvert attaches (figure 7). In the left center of the mound is a narrow, elongate opening leading from the introvert to a small pouch into which the true mouth protrudes. A narrow, thick-walled tube leads from the mouth to the buccal cavity, a distance of about 9 mm, of which the first 6 mm run to the right through the posteroventral wall of the proboscis bulb.



Figures 2, 3. *Pleioptygma helenae.* **2.** Diagrammatic sketch of animal of 69 mm specimen removed from shell, right lateral and dorsal views. **3.** Diagrammatic sketch of foregut of 69 mm specimen. Structures not in life positions. bm, buccal mass; es, esophagus; f, foot; hg, hypobranchial gland; in, introvert; m, muscular mantle edge; pb, proboscis bulb; rs, radula sac; s, siphon; ug, unpaired foregut gland

The buccal mass walls are very thick, ranging from about 3 mm at the anterior end to about 1.5 mm near the opening of the esophagus (figure 8). The buccal cavity is spacious, and its floor has a prominent transverse ridge just posterior to the oral tube opening. The opening of the radula sac is subrectangular and is located in the center of the buccal cavity floor. The radula sac is broad, comprising the posteroventral ⅔ of the buccal mass. Just behind and above the posterior edge of the radula sac opening is a small (2 mm long, 1 mm wide) caecum. Directly above the caecum is the opening of the anterior esophagus.

Radula: The triserial ribbon is broad and short (length : width = 1.3–1.6:1), about 5% of shell length, with about 70–100 transverse rows of teeth (figures 9–11). The posterior 60% of the rows are above the bending plane, the anterior 40% below. The rhachidian teeth of the larger specimen are 1.05 mm wide and the lateral teeth are 1.30 mm wide at the bending plane. The rhachidian and lateral teeth are similar in structure, each having a broad, narrow basal plate and numerous equal, sharp, narrowly triangular cusps (the rhachidian tooth has about 25 cusps, the lateral teeth about 35).

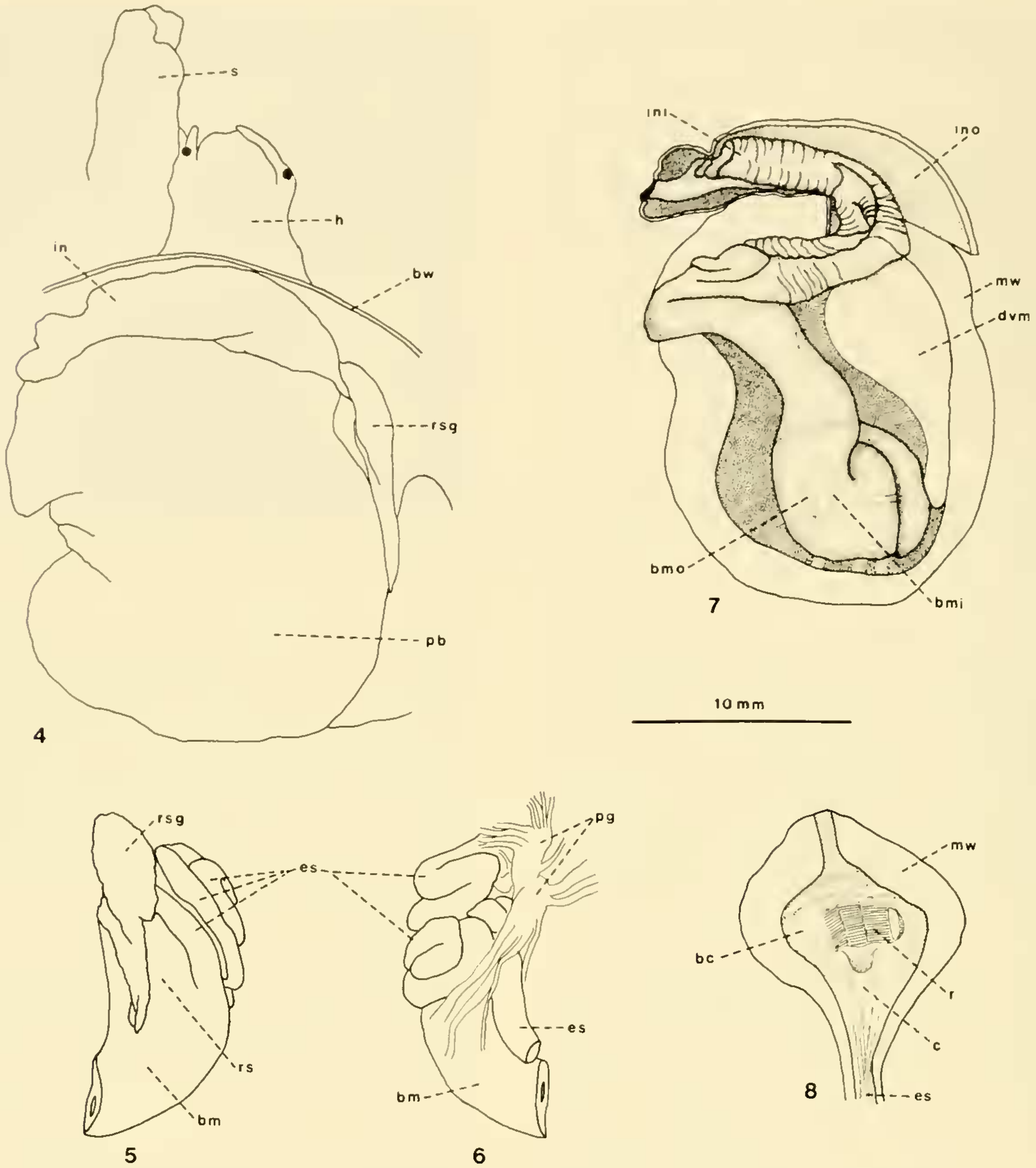
Esophagus: Upon exiting the buccal cavity, the esophagus curves slightly to left, makes a 180° ventral turn and runs underneath itself for about 5 mm, continues through the nerve ring and turns upward, forms a convoluted mass of half-loops, and finally runs posteriorly and diagonally to the left beneath the proboscis bulb (figures 5, 6). A valve of Leiblein was not found.

Salivary glands: These glands are elongate, roughly lanceolate organs lying along either side of the radula sac and are fused at the broad ends (figures 4, 5). The salivary ducts are short and do not pass through the nerve ring; the right duct enters the right side of the radula sac just posterior and ventral to the external separation of the esophagus from the buccal mass; the left duct enters on the left side slightly more ventrally than does the right duct. No accessory salivary glands were observed.

Unpaired foregut gland: The duct is long (about 25 mm), and coiled into a ball to the right of the buccal mass (figure 3). The duct terminates in a muscular, lanceolate bulb 4 mm long and 1.8 mm in greatest width. This organ was found only in the smaller specimen, and the connection of the duct with the foregut was not found.

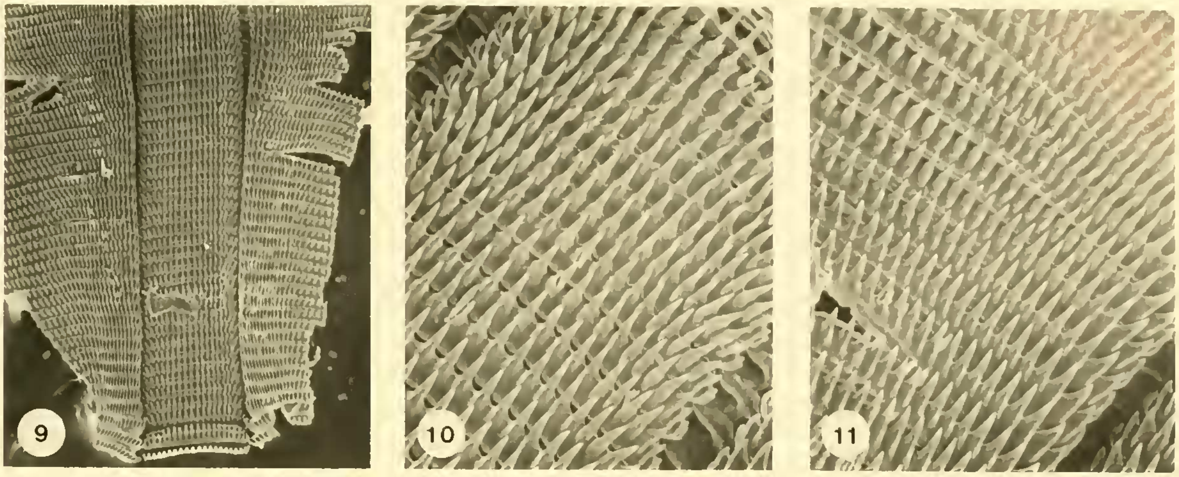
DISCUSSION

Familial placement of *Pleioptygma* has always been controversial. Conrad (1840) first described the type species of *Pleioptygma* as *Voluta* but soon (Conrad, 1842) transferred the species to *Mitra*, a placement followed by Tuomey and Holmes (1856). However, Conrad (1863) seemingly reversed himself by assigning his new genus *Pleioptygma* to Volutidae. Heilprin (1887) ignored *Pleioptygma* and maintained the species group in *Mitra*. Dall (1890) noted Conrad's placement of *Pleioptygma* in Volutidae but treated it as a subgenus of *Mitra*, a classification followed by Cossmann (1899), Tucker and Wilson (1933), Gardner (1937), Mansfield (1937), Olsson and Harbison (1953), and Dubar (1958, 1962). Cernohorsky (1970:61) stated unequivocally that *Pleioptygma* was not referable to Mitridae but instead possessed many features "all consistent with the Volutidae. An assignment to the Scaphellinae might be appropriate." Radwin and Bibbey (1972:95–96) rejected that placement, stating that characters Cernohorsky (1970) used to exclude *Pleioptygma* do occur in some Mitridae, and concluded: "We are thus tentatively placing the subgenus *Pleioptygma* in the Mitridae, pending examination of the radular dentition of *M.* (*P.*) *helenae*." Cernohorsky (1976: 282) ignored Radwin and Bibbey and maintained that



Figures 4–8. *Pleioptygma helenae*. Foregut morphology of 107 mm specimen. **4.** Diagrammatic sketch of proboscis complex in relation to head, cephalic cavity opened dorsally. **5, 6.** Diagrammatic sketches of buccal mass and associated organs. **5.** Dorsal (morphological right side) view. **6.** Ventral (morphological left side) view. **7.** Dissection of proboscis bulb and introvert, opened dorsally. **8.** Dissection of buccal mass, opened dorsally. bc, buccal cavity; bm, buccal mass; bmi, inner opening to buccal mass; bmo, outer opening to buccal mass; bw, body wall; c, caecum of buccal mass; dvm, dorsoventrally oriented muscle mass; es, esophagus; h, head; in, proboscis introvert; ini, inner tube of introvert; ino, outer tube of introvert; mw, muscular wall of proboscis bulb; pb, proboscis bulb; pg, pedal ganglia; r, radula; rs, radula sac; rsg, right salivary gland; s, siphon.

"shell features of *Pleioptygma* are consistent with the Volutidae, and the genus should be referred to the Volutid subfamily Scaphellinae." Weaver and duPont (1970) omitted *Pleioptygma* from their monograph of worldwide Volutidae. In all cases, judgments of affinities of *Pleioptygma* were based entirely on shell characters. Although by no means complete, the anatomical data presented above provide an opportunity to re-evaluate the relationships of *Pleioptygma*. The following discussion compares the anatomy of *Pleioptygma helenae* with that of the Mitridae, Costellariidae, and Volutidae, the families to which *Pleioptygma* has traditionally been assigned, and the Turridae, a group that has some superficial similarities of foregut anatomy to that of *Pleioptygma*. Table 1 summarizes the comparison of characters of *Pleioptygma* and the four families cited above.



Figures 9–11. *Pleioptygma helenae*. SEM micrographs of radula. **9.** View of portion of intact ribbon. × 25. **10.** Rhachidian teeth. × 100. **11.** Lateral teeth. × 100.

Ponder (1972) investigated the anatomies of several mitriform gastropods from the southwestern Pacific. In that study, he found that the Mitridae, as then perceived, actually comprised two families, the Mitridae *sensu stricto* and the Costellariidae (as Vexillidae). I am here following that decision and will compare *Pleioptygma* to each group separately. Terminology of anatomical structures follows Ponder's (1973) review of the comparative anatomy of the Neogastropoda. The shells of the Mitridae and *Pleioptygma* are rather similar in shape and sculpture, with spiral ridges predominating; however, the shells of *Pleioptygma* are larger and lighter. The radulae of the two groups are also quite similar, both having comb-like lateral teeth and multicuspid rhachidian teeth (except in *Pterygia*, which lacks lateral teeth). *Pleioptygma*, however, has hypertrophied rhachidian teeth that are only slightly less broad than the lateral teeth. Mitrids, on the other hand, have rhachidian teeth that are noticeably narrower than the lateral teeth. The radula of *Mitra sigillata* Azuma, 1965 (Cernohorsky, 1970, fig. 26), is most similar to that of *P. helenae* in that the rhachidian has about 20 cusps and the laterals have about 22. However, the rhachidian is only about 60% of the width of the laterals, compared to 80% in *P. helenae*. The soft parts of *Pleioptygma* offer a number of important characters that differ from the Mitridae. The foot of *Pleioptygma* is relatively large, whereas that of mitrids is small. The head of *Pleioptygma* has a distinct, relatively large snout; that of the Mitridae has no such structure. An epiproboscis, one of the hallmarks of the Mitridae, is missing in *Pleioptygma*. The proboscis mouth of mitrids has a strong, muscular sphincter, the "peristomal rim" of Ponder (1972). In *Pleioptygma* the proboscis "mouth" has no such rim, the opening of the snout having assumed that function. In fact, the true mouth of *Pleioptygma* has been divorced from the extensible portion of the proboscis. Mitrids have a proboscis sac, but it is a very thin-walled structure, in contrast with the extremely thick-walled, muscular proboscis bulb of *Pleioptygma*; however, it is not yet possible to determine whether the two structures are homologous. The prominent unpaired foregut gland of *Pleioptygma* is totally absent in the Mitridae.

Members of the Costellariidae differ from *Pleioptygma* in the following characters: 1) axial, rather than spiral, shell sculpture is predominant; 2) lateral teeth of the radula are simple and sickle-shaped; 3) the rhachidian is much narrower; 4) an introvert and proboscis bulb are absent; 5) a pair of accessory salivary glands is present; and 6) an unpaired foregut gland is present, but it comprises only the Gland of Leiblein (see Ponder, 1972).

The volutids are distinguished from *Pleioptygma* by the following characters: 1) the dominant shell sculpture, when present, is axial; 2) the radula is usually uniserial with a uni-, tri-, or multicuspid rhachidian that is comparatively much smaller; 3) siphonal appendages are present; 4) an introvert is absent; 5) there is no proboscis bulb; 6) paired accessory salivary glands are present; and 7) an unpaired foregut gland is present but comprises only the Gland of Leiblein.

The proboscis complex of *Pleioptygma* is superficially similar to that of some turrids, particularly to some members of the subfamily Daphnellinae (Smith, 1967). In the Turridae, the buccal mass has also been divorced from the proboscis tip; there is an introvertible proboscis, at least in *Philbertia* (Smith, 1967); and the poison gland resembles the unpaired foregut gland of *Pleioptygma*. However, the proboscis bulb of *Pleioptygma* and the hypertrophied rhachidian teeth with comb-like laterals are not similar to any described turrid, and most of the similarities in other structures are analogous, not homologous.

Considering the anatomical differences separating *Pleioptygma* from other similar neogastropod families, it is evident that *Pleioptygma* cannot be accommodated in any defined family. Therefore, I propose that *Pleioptygma* represents a family separate from other mitriform gastropods, defined principally by the autapomorphous proboscis complex, the position of the buccal mass, and the hypertrophied rhachidian tooth. The morphologies

Table 1. Comparison of shell and anatomical characters of Pleioptygmatidae, Mitridae, Costellariidae, Volutidae, and Turridae. Characters of Mitridae and Costellariidae from Ponder (1972, 1973); Volutidae from Clench and Turner (1964) and Ponder (1973); and Turridae from Smith (1967).

Character	Pleioptygmatidae	Mitridae	Costellariidae	Volutidae	Turridae
Shell size	Medium to large	Medium to large	Small to large	Small to large	Small to large
Predominant sculpture	Spiral	Smooth or spiral	Axial	Smooth or axial	Smooth, axial or spiral
Radula					
Lateral teeth	Multicuspid	Multicuspid or absent	Simple, curved	Usually absent	Usually absent, multicuspid if present
Rhachidian teeth	Wide multicuspid	Usually relatively small, multicuspid	Relatively large, 3 or more cusps	Small to large, uni-, tri-, or multicuspid	Usually absent, rudimentary if present
Foot	Large relative to shell	Small relative to shell	Moderate relative to shell	Large relative to shell	Small relative to shell
Siphonal appendages	Absent	Absent	Absent	Present	Absent
Alimentary canal					
Proboscis	Introvert	Pleurembolic	Pleurembolic	Pleurembolic	Polyembolic or intraembolic
Proboscis bulb	Present	Absent	Absent	Absent	Absent
Epiproboscis	Absent	Present	Absent	Absent	Absent
Mouth	At base of proboscis complex, no peristomal rim	At tip of proboscis, with peristomal rim	At tip of proboscis, no peristomal rim	At tip of proboscis	At base of proboscis, with peristomal rim
Accessory salivary glands	Absent?	Absent	Present, paired	Present, paired	Usually absent, paired if present
Unpaired foregut gland	Present	Absent	Present	Present	Present, poison gland
Valve of Leiblein	Absent	Small or absent	Large	Large	Absent

of radula and shell suggest that the Pleioptygmatidae may be derived from an ancestor in common with the Mitridae.

The function of the proboscis complex of *Pleioptygma* can only be surmised. In both specimens dissected for this study, the anterior portion of the introvert was lying free in the cephalic cavity, wedged between the anterior face of the proboscis bulb and the body wall. Evidence was lacking of any previous attachment to the walls of the snout. This position may have been the result of extreme retraction in response to contact with the preservative. In life, the introvert probably lies partially within the snout and is everted by a combination of contractions of the intrinsic circular muscle of the introvert and muscular contraction of the proboscis bulb. The length of the everted introvert must be quite extensive, as the wrinkled and folded appearance of the contracted organ indicates. The length of the introvert, combined with the dissociation of the radula from the proboscis complex, suggests that *Pleioptygma helenae* feeds on soft-bodied prey, probably tubicolous and crevice-dwelling worms such as sipunculans and polychaetes. The position of the radula suggests that it acts principally in triturating prey and transferring food into the esophagus.

Two major differences were observed between the two specimens. The presence of an unpaired foregut gland in the smaller specimen, but not in the larger, cannot be explained. Differences in the length and morphological relationship of the introvert and proboscis bulb, as well as the morphological relationship of the proboscis bulb and buccal mass, may be explained by ontogenetic changes. Apparently, the total length of the introvert develops relatively early in ontogeny, at least by the time the shell reaches a length of about 70 mm. With growth, the length remains about the same, but the width increases. Increasing the volume of the lumen of the proboscis bulb also allows the enclosed introvert to become less convoluted. In a similar manner, growth of the proboscis bulb, especially the thickening of the bulb walls, encroaches upon and eventually envelops the morphological anterior end of the buccal mass, creating the mound on the floor of the proboscis bulb.

ACKNOWLEDGEMENTS

I thank Mr. Louis Kotora, who provided the two specimens of *Pleioptygma helenae*, and William G. Lyons, who allowed me to perform the dissections, provided the shell photographs, and made valuable comments on the manuscript. Thomas H. Perkins, David K. Camp, Dan C. Marelli, and two anonymous reviewers also provided critical comments on the manuscript.

LITERATURE CITED

Cernohorsky, W. O. 1970. Systematics of the families Mitridae and Volutomitridae (Mollusca: Gastropoda). Bulletin of the Auckland Institute and Museum 8:1–190.

Cernohorsky, W. O. 1976. The Mitridae of the world. Part I. The subfamily Mitrinae. Indo-Pacific Mollusca 3(17): 273–528.

Clench, W. J. and R. D. Turner. 1964. The subfamilies Volutinae, Zidoninae, Odontocymbiolinae and Calliotectinae in the western Atlantic. Johnsonia 4(43):129–180.

Conrad, T. A. 1840. New fossil shells from N. Carolina. American Journal of Science 39(2):387–388.

Conrad, T. A. 1842. Observations on the Secondary and Tertiary formations of the southern Atlantic states; by James T. Hodge. With an appendix by T. A. Conrad. American Journal of Science 42(2):344–348.

Conrad, T. A. 1863. Catalogue of the Miocene shells of the Atlantic slope. Proceedings of the Academy of Natural Sciences of Philadelphia 14(10–12):559–583.

Cossmann, A. E. M. 1899. Essais de paléoconchologie comparée, Vol. 3. Paris, 201 p.

Dall, W. H. 1890. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene Silex-beds of Tampa and the Pliocene beds of the Caloosahatchee River. Part I. Pulmonate, Opisthobranchiate and Orthodont gastropods. Transactions of the Wagner Free Institute of Science of Philadelphia 3(1):1–200.

DuBar, J. R. 1958. Stratigraphy and paleontology of the Late Neogene strata of the Caloosahatchee River area of southern Florida. The Florida Geological Survey, Geological Bulletin 40:1–267.

DuBar, J. R. 1962. Neogene biostratigraphy of the Charlotte Harbor area in southwestern Florida. The Florida Geological Survey, Geological Bulletin 43:1–83.

Gardner, J. 1937. The molluscan fauna of the Alum Bluff Group of Florida. Part VI. Pteropoda, Opisthobranchia and Ctenobranchia (in part). United States Geological Survey Professional Paper 142-F:251–435.

Heilprin, A. 1887. Explorations on the west coast of Florida and in the Okeechobee wilderness. With special reference to the geology and zoology of the Floridian Peninsula. Wagner Free Institute of Science of Philadelphia, Philadelphia, PA, vi + 134 p.

Houbrick, R. S. 1986. Discovery of a new living *Cerithioclava* species in the Caribbean (Mollusca: Prosobranchia: Cerithiidae). Proceedings of the Biological Society of Washington 99(2):257–260.

Mansfield, W. C. 1937. Mollusks of the Tampa and Suwannee Limestones of Florida. The Florida Geological Survey, Geological Bulletin 15:1–334.

Olsson, A. A. and A. Harbison. 1953. Pliocene Mollusca of southern Florida with special reference to those from North Saint Petersburg with special chapters on Turridae, Vitrinellidae and fresh-water mollusks. The Academy of Natural Sciences of Philadelphia, Monographs 8:v + 457 p.

Petuch, E. J. 1981. A volutid species radiation from northern Honduras, with notes on the Honduran Caloosahatchian Secondary Relict Pocket. Proceedings of the Biological Society of Washington 94(4):1110–1130.

Petuch, E. J. 1982a. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. Palaeogeography, Palaeoclimatology, Palaeoecology 37:277–312.

Petuch, E. J. 1982b. Paraprovincialism: remnants of paleoprovincial boundaries in Recent marine molluscan provinces. Proceedings of the Biological Society of Washington 95(4):774–780.

Ponder, W. F. 1972. The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems. Malacologia 11(2):295–342.

Ponder, W. F. 1973. The origin and evolution of the Neogastropoda. Malacologia 12(2):295–338.

Ponder, W. F. and A. Warén. 1988. Appendix. Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. *In:* Ponder, W. F. (ed.). Prosobranch phylogeny. Proceedings of a symposium held at the 9th International Malacological Congress, Edinburgh, Scotland, August 31–September 6, 1986. Malacological Review, Supplement No. 4:288–317.

Quinn, J. F., Jr. and W. G. Lyons. 1984. A partial description of the anatomy of *Pleioptygma helenae* (Gastropoda: Neogastropoda). American Malacological Bulletin 3(1):97–98 (abstract).

Radwin, G. E. and L. J. Bibbey. 1972. A new mitrid from the western Atlantic. Transactions of the San Diego Society of Natural History 17(7):95–99.

Smith, E. H. 1967. The proboscis and oesophagus of some British turrids. Transactions of the Royal Society of Edinburgh 67(1):1–22.

Tucker, H. I. and D. Wilson. 1933. A second contribution to the Neogene paleontology of South Florida. Bulletins of American Paleontology 18(66):1–21.

Tuomey, M. and F. S. Holmes. 1855–1857. Pleiocene fossils of South-Carolina containing descriptions and figures of the Polyparia, Echinodermata and Mollusca. Russell and Jones, Charleston, SC, xvi + 152 p.

Weaver, C. S. and J. E. duPont. 1970. Living volutes. A monograph of the Recent Volutidae of the world. Delaware Museum of Natural History, Monograph Series No. 1:xv + 375 p.